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THE RED-FRUITED CROWBERRIES IN NORTH AMERICA

DORIS LÖVE

HISTORY

The first time red-fruited crowberries are mentioned in North American botanical literature seems to be in La Pylaie's (1825) "Notice sur l'île de Terre-Neuve et quelques îles voisines". They were found growing on top of low mountains on Ile Saint-Pierre, later also on Miquelon. Identifying them as *Empetrum rubrum* Willd., La Pylaie stated: "Cette plante est identique avec les échantillons magellaniques conservés dans l'herbier de M. Jussieu" (p. 426, l. c.).

Empetrum rubrum was described by Willdenow (1805) from plants collected along Magellan Straits in South America (map, fig. 1), and distinguished from the Linnean *E. nigrum* by its red fruits, hairy branches and scabrous leaves. Though La Pylaie did not mention that his species had hairy branches, it was later confirmed that such was the case (Fernald & Wiegand, 1913).

In many places in his travelogue La Pylaie stated that ordinary "*E. nigrum*" was abundant and common in Newfoundland, and he never indicated that this species was different from what he already knew from his native France. It also seems that he did not find any red-fruited plants on Newfoundland proper as is indicated on p. 493 (l. c.): "... une pelouse composée de l'*E. nigrum* (l'*E. rubrum* a disparu depuis l'île de Miquelon), ...".

Rafinesque (1838), always eager to disagree and argue, was of a different opinion, however, as to the identity of the red crowberries. He apparently had not seen the actual specimens of La Pylaie, possibly not even read his paper

properly, but had studied a specimen of crowberry with red fruits from "Labrador". No mention is made in the "New Flora of North America" (Rafinesque, 1838) to the collector of this specimen, or from where in "Labrador" it emanated. Describing the specimen, Rafinesque (l. c.) wrote in one place: ". .berry purple. .", in another: "My specimen is from Labrador and has red berries strikingly like those of *Phytolacca!*". Somewhat further on he declared: "My sp. is perfectly distinct, the branches are terete smooth but sulcate among the leaves. . ." (all p. 50, l. c.).

He named his plant *Empetrum purpureum* and made La Pylaie's *E. rubrum* a synonym of this. As area for his new species he indicated all the then known area of "*E. nigrum*" in North America: "Canada, Labrador, New Foundland, White Mts., Lake Superior, near rocky shores". This he did because he quite boldly concluded that all *Empetrum* of this continent should have red fruits, and because he was convinced that Michaux (1803) and "all Am. botanists after him" were wrong in referring the American plants to the black-fruited European *E. nigrum* L.

It seems that Rafinesque, though in part mistaken, nevertheless was aware that the American crowberries were different from typical European *E. nigrum* L. He even suspected that in the European Alps and in Siberia there existed black-fruited plants which approached more closely the American ones than *E. nigrum* L. The characters, mainly leaf-differences, on which he based his assumptions, are, however, not sufficient for a distinction between what we today recognize as the two species *E. nigrum* L. and *E. hermaphroditum* (Lge.) Hagerup. The latter, quite correctly, occurs in the Alps (Favarger, Richard, & Duckert, 1959) as well as all over boreal and arctic North America and Siberia (Vassiliev, 1949; Löve & Löve, 1959). Rafinesque (1838) erred, however, in respect to the color of the fruit: black is predominant in North America, red is rare, and found only in certain areas. But he was right in distinguishing the northern crowberries from the South American *E. rubrum*.

After Rafinesque (1838) the existence of North American red-fruited crowberries seems to have been forgotten during

the rest of the 19th century, with the exception of a brief mention of such plants from Greenland by Durand in 1863

Durand (in Durand, James, & Ashmead, 1863) listed a number of plants from northwest Greenland, collected in 1861 by Dr. I. I. Hayes between the 78th and 82nd parallels. Among these was "*E. rubrum* Willd. (a variety of *E. nigrum*?)" from Tessuissak. The listing is accompanied by the following foot-note: "Drupe red, stems apparently smaller and more decumbent than in *E. nigrum*, from which it does not otherwise differ. It is a remarkable fact of geographical botany, that this red-fruited species, originally found on the shores of the Straits of Magellan, should appear again at the opposite extremity of the American continent. Messrs. La Pylaie and Tuckerman met with it in Newfoundland, and, quite lately Abbé Ferland, a Catholic missionary of Laval University of Quebec, found it likewise on the coast of Labrador together with *Empetrum nigrum*." (p. 95, (l. c.).

On this one must comment that it is not known that Tuckerman ever visited Newfoundland (Dr. E. Rouleau, pers. comm.). Abbé Ferland's plants were collected in 1858 at La Tabatière, North Shore of St. Lawrence Gulf in Quebec province not far from the present border of Labrador (Brunet, 1863, 1867). We have not been able to locate this collection, but Fernald (1923) refers it without further explanation to *E. Eamesii*.

As Durand's (1863) list dealt with plants from Greenland, it of course did not concern the scientists dealing with the American flora further south. It seems that we owe the rediscovery of red-fruited crowberries on the American continent and the re-opening of the discussion of their taxonomy to Fernald, who, together with C. H. Knowlton, found such plants on Mt. Saddleback, Maine, in 1894 (Fernald, 1902).

At first Fernald (1902) associated these plants with the Chilean *rubrum*-complex as being identical with *E. nigrum* v. *andinum* DC. (cf. De Candolle, 1869). Later, when he had seen considerably more material from both Newfoundland, Canada, and New England, Fernald together with Wie-

gand (1913) separated the North American ones from the South American and placed the former into two distinct, red-fruited species, *E. atropurpureum* Fern. & Wieg. and *E. Eamesii* Fern. & Wieg. Eames, for whom the Newfoundland

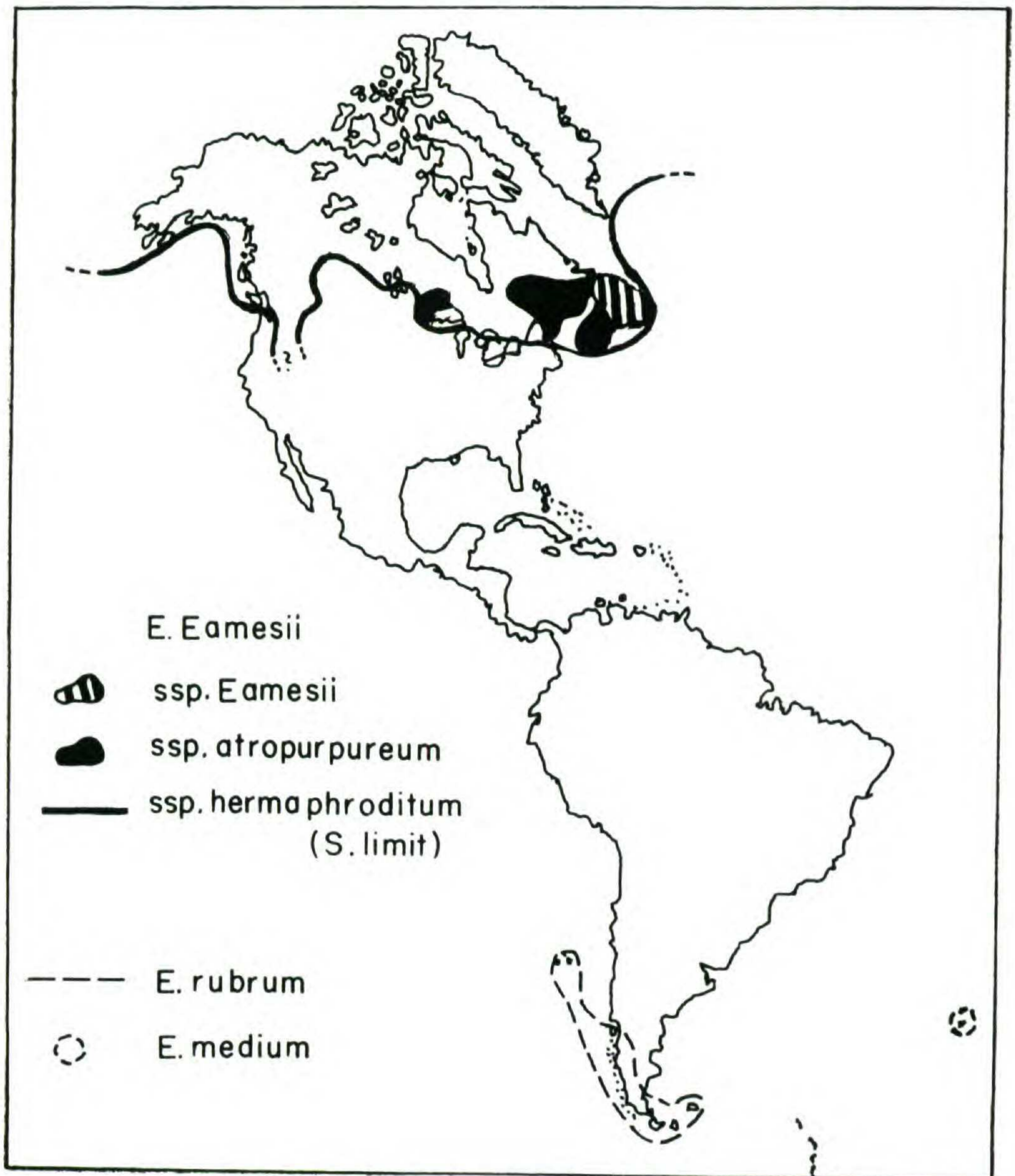


FIG. 1. Map of the distribution in North America of *Empetrum Eamesii* ssp. *Eamesii*, ssp. *atropurpureum* and ssp. *hermaphroditum*, and in South America of *E. rubrum* and *E. medium*.

plants were named, had already pointed out in 1909 that these were quite remote from the South American species, and also, which is very important, remarked that his plants were polygamous (Eames, 1909).

In their paper Fernald and Wiegand (1913) included, though somewhat reluctantly, an arctic *E. nigrum* v. *purpureum* (Raf.) Fern. & Wieg. based upon the records of Rafinesque (1838) and Durand (1863) as well as a report about such plants on Ellesmereland by Simmons (1906).

In spite of the fact that Fernald and Wiegand (1913) had definitely dissociated *E. atropurpureum* and *E. Eamesii* from the South American *E. rubrum* and its varieties, Good (1927) in his large and thorough monograph of the genus *Empetrum* re-established the bond, making *atropurpureum* a variety and *Eamesii* a subspecies of *E. rubrum*. He also mentioned Rafinesque's *purpureum*, partly as a synonym of his ssp. *Eamesii*, partly as a special form of his *E. nigrum*.

It should be noted here that Good (1927) for his *E. rubrum* preferred the author-name "Vahl" instead of "Willd." There seems, however, to be no doubt that Willdenow described this species and is the rightful author of its name (Willdenow, 1805), even if he referred in his description to "*E. rubrum*. Vahl in litt." This remark does not validate Vahl as the author of the species, and we will continue to use the legal and otherwise widely accepted author-name Willdenow.

OBSERVATIONS

Sex of the flowers: Good (1927) made a very thorough study of growth habit, leaf morphology, hairiness, flower structure and fruit color throughout the genus *Empetrum*, but he, as most preceding students of this genus, failed to understand the importance of the sex of the flowers, though he always reported it.

Apparently Linnaeus (1753) knew only the dioecious type of *Empetrum*, but Willdenow (1805) noted that Jacquin had collected hermaphroditic specimens and that he himself had seen one such sheet at Uppsala. De Candolle (1869) stated that *Empetrum* is sometimes dioecious, sometimes monoecious, and that the female flowers carry traces of stamens, the male flowers rudimentary ovaries (cf. also Hagerup, 1922).

In 1880 J. Lange had already named plants from Greenland as *E. nigrum* β *hermaphroditum*, but without any description. Warming (1887), Samuelsson (1913), Mentz

(1919), and Hagerup (1927) found plants with bisexual flowers to be common in the Arctic and in northern Scandinavia, the dioecious ones common in more southern regions (cf. also Hagerup, 1922). The existence of hermaphrodites in the Alps (Favarger, Richard & Duckert, 1959) and in northern Siberia (Vassiliev, 1949) has also been amply verified.

Hagerup (1927) was able to take one step further than his contemporaries by studying the chromosomes of the two types of *Empetrum*, and he found that the dioecious plants were diploid with $2n=26$, those with hermaphroditic flowers were tetraploid with $2n=52$ chromosomes. Because of this Hagerup (1927) described the hermaphroditic form and raised it to specific status, *E. hermaphroditum* Hagerup. Since then, the chromosome number $2n=52$ has been confirmed in this species from several localities in Europe and the Arctic (Arwidsson, 1938; Flovik, 1940; Löve, in Arwidsson, 1943; Löve & Löve, 1956; Favarger, Richard & Duckert, 1959) as well as in North America (Löve & Löve, 1959).

It must be noted in this connection that it is quite usual to find polygamous specimens among the tetraploid ones (cf. also De Candolle, 1869; Samuelsson, 1913; Hagerup, 1927; Porsild, 1957; Löve & Löve, 1959) and sometimes, but very rarely, also in the dioecious ones (Samuelsson, 1913; Blackburn, 1938). It seems to this author that this phenomenon occurs more frequently in the southern part of the distribution area of *E. hermaphroditum* than in the really arctic parts of it. Whether this is a sign of instability in the sex determining mechanism or a reaction due to differences in day-length has yet to be established.

Samuelsson (1913) reported on a specimen of *E. nigrum* from Jämtland, Sweden (63° N. Lat.) which in the first year, 1908, after transplantation to Uppsala ($59^{\circ} 45'$ N. Lat.) produced male flowers (the flowers are already completed in the buds a season before flowering), but later, in 1910, appeared polygamous with most of the flowers female. Blackburn (1938) found a hermaphroditic, diploid plant in Scotland. As it had three stamens, (six is the more common in true *E. hermaphroditum*; cf. Hagerup, 1927) and further-

more looked morphologically like *E. nigrum*, Blackburn's specimen must be considered as an abnormal form of *E. nigrum*. The development of rudimentary stamens or ovaries (such as found in *E. nigrum*) into functional ones, naturally

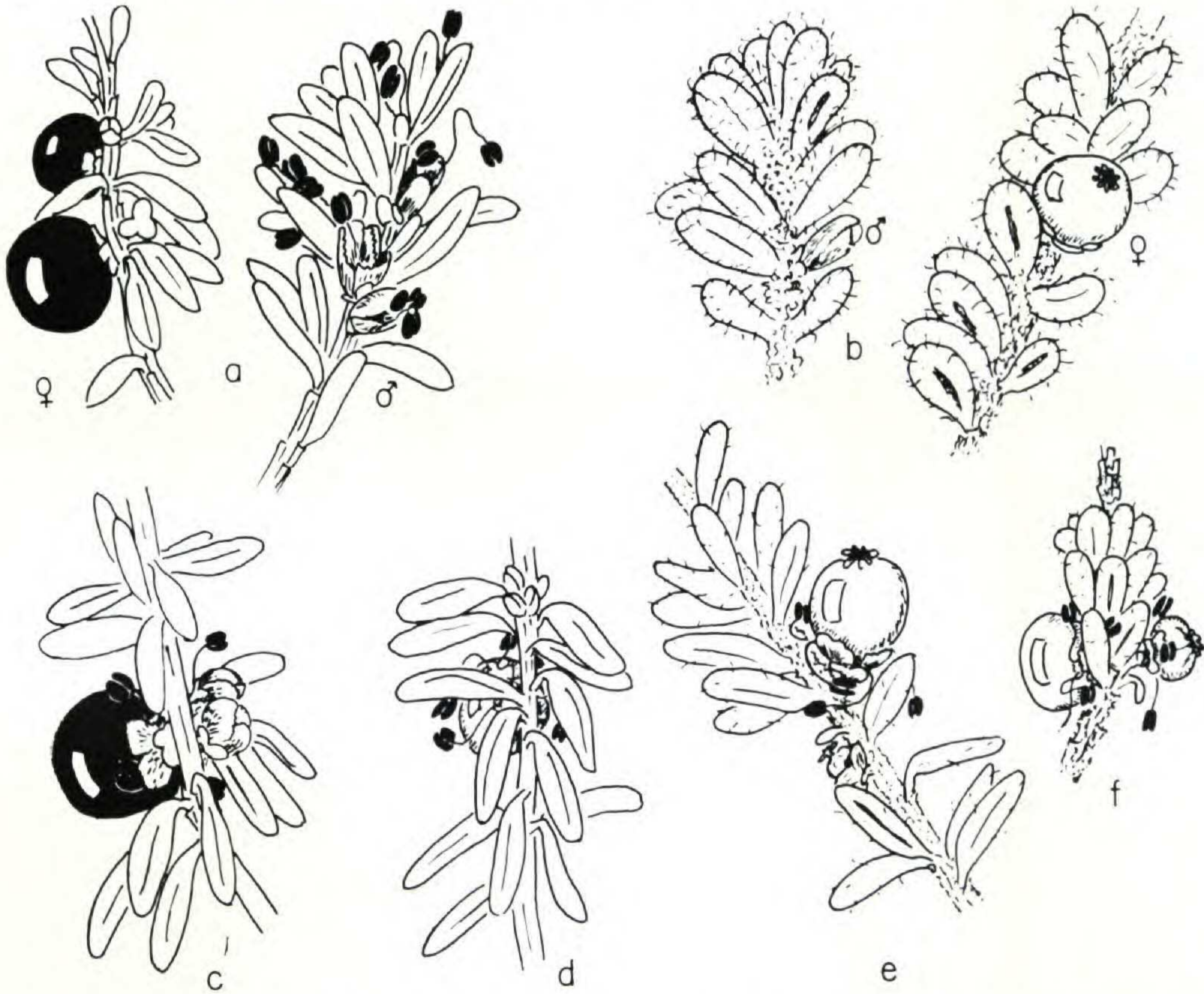


Fig. 2. Drawings of flowering twigs of *Empetrum*: a) ♀ and ♂ of *nigrum*, b) ♂ and ♀ of *rubrum*, c) ♀ of *hermaphroditum*, d) ♀ of "*purpureum*", e) ♀ of *atropurpureum*, and f) ♀ of *Eamesii*.

or after a fungus attack, is not unknown in other dioecious species (D. Löve, 1940, 1942, 1944, 1952).

Both Good (1927) and Hagerup (1927) agreed that the red-fruited South American *E. rubrum* is dioecious, but Good (l. c.) also found "aberrant" specimens with long-petioled, larger, apiculate leaves and brown-hairy stems from Tristan da Cunha and Gough Island to be hermaphroditic (*E. rubrum* Vahl f. *medium* (Carm.) R. Good). Unfortunately, nothing is known regarding the chromosome numbers in the *E. rubrum* complex. If the situation in the Southern Hemisphere parallels that of the Northern, it seems likely that the dioecious and hermaphroditic taxa in the South-

ern Hemisphere should also have different levels of ploidy, and that the hermaphrodites should rather be regarded as a separate species, *E. medium* Carm.

Good (1927) stated further that his *E. rubrum* ssp. *Eamesii* from Labrador, Newfoundland and Saguenay as well as two specimens thereof from Fuegia and Juan Fernandes, "the latter of doubtful color", had unisexual flowers, and that his *E. rubrum* v. *atropurpureum* had unisexual and polygamous flowers (regarding our opinion of the true distribution of *E. Eamesii*, cf. maps in figs. 1 and 5).

The present author has, however, investigated a very large number of herbarium specimens of both *E. Eamesii* and *E. atropurpureum* and found them as a rule to be hermaphroditic (cf. fig. 2), but occasionally polygamous, carrying a number of purely female flowers on the same bush as the hermaphroditic flowers. The specimens of *E. purpureum*, seen by us (fig. 2) and by Dr. J. Lid, Oslo, Norway, have only hermaphroditic flowers.

In the case of polygamy it is often hard to judge from pressed specimens whether the "purely" female flowers have lost their stamens by handling, or after the fruits were ripe, or if they never had any, but opening a number of buds and studying the intact flower has convinced this author that truly female flowers occur on otherwise hermaphroditic specimens. This has been observed in North American red- and black-fruited crowberries (cf. also Löve & Löve, 1959).

In all cases both black- and red-fruited crowberry-bushes from North America carry a multitude of fruits, which is in marked contrast to the few-fruited bushes of *E. nigrum* (pers. observation; cf. also Hagerup, 1927).

Hairiness: Another character which has often been used for associating the North American and South American taxa is the hairiness coating the young twigs and sometimes also the leaves of the red-fruited forms, in contrast to the entirely glabrous twigs and leaves of *E. nigrum* and *E. hermaphroditum* (Willdenow, 1805; De Candolle, 1869; Fernald, 1902; Fernald & Wiegand, 1913; Hagerup, 1927; Good, 1927).

Although *E. nigrum* and *E. hermaphroditum* in the strict sense can be considered essentially glabrous (fig. 2a, c), taxa are known from both species, in their wide sense, which display more or less hairiness at least on the young twigs. Thus, Vassiliev (1949) described three taxa of the *nigrum* complex as hairy: *E. sibiricum* V. Vassil. with young branches more or less covered with reddish or whitish, short, curly hairs; *E. kurilense* V. Vassil. with reddish, curly hairs on the one year old branches; and *E. Kardakovii* V. Vassil. (with red fruits, but dioecious) with reddish or whitish, usually curly hairiness. The latter species is found in Kamchatka and around the Bering Sea (cf. Vassiliev, 1949). *E. arcticum*, V. Vassil., of the *hermaphroditum*-group, has twigs "with a red fluff".

In all species of *Empetrum*, the bud scales are normally hairy (pers. observation; Hagerup, 1922, 1927).

As a rule the southern taxa can be considered as hairy (fig. 2b), but in the South American *rubrum*-complex the hairiness tends to vary from glabrescent (*E. rubrum* f. *andinum* (Phil.) Good) to a dense, felty tomentum (*E. rubrum* f. *falklandicum* Good), according to Good (1927).

In most cases the hairs on the leaves of the South American taxa, particularly those along the "leaf corners", are persistent, which is not the case in the northern taxa. *E. Eamesii* and *E. atropurpureum* both have distinctly hairy young twigs, but the sparse hairiness on the young leaves falls off rather soon (fig. 2e, f). The hairiness of the northern taxa is always soft, never scabrous, as indicated for *E. rubrum* by Willdenow (1805).

E. purpureum from Canadian Arctic is always glabrous (pers. observation; also fide J. Lid, Oslo, Norway, for the plants from Ellesmereland).

The leaves: The word "leaf corner" was used above in preference to "margin", as the *Empetrum* leaf has a peculiar structure (De Candolle, 1869; Menz, 1912; Hagerup, 1927). The true, and always hairy, margins meet on what appear to be the underside of the leaf, often giving the impression of a nerve sunk in a crevice (fig. 3). The really abaxial side of

the leaf is, however, enclosed in its protected hollow and carries glands and stomata, whereas the adaxial side has no stomata and is covered by a more or less heavy wax-coating (fig. 4). The wax-coating on the *E. rubrum* leaves studied by this author seems to be much thicker than that on specimens from the Northern hemisphere (fig. 4). Whether this is a persistent feature throughout the *rubrum*-complex is not known.

Studying sections of *Empetrum* leaves from both the Northern and Southern Hemisphere and of black- as well as

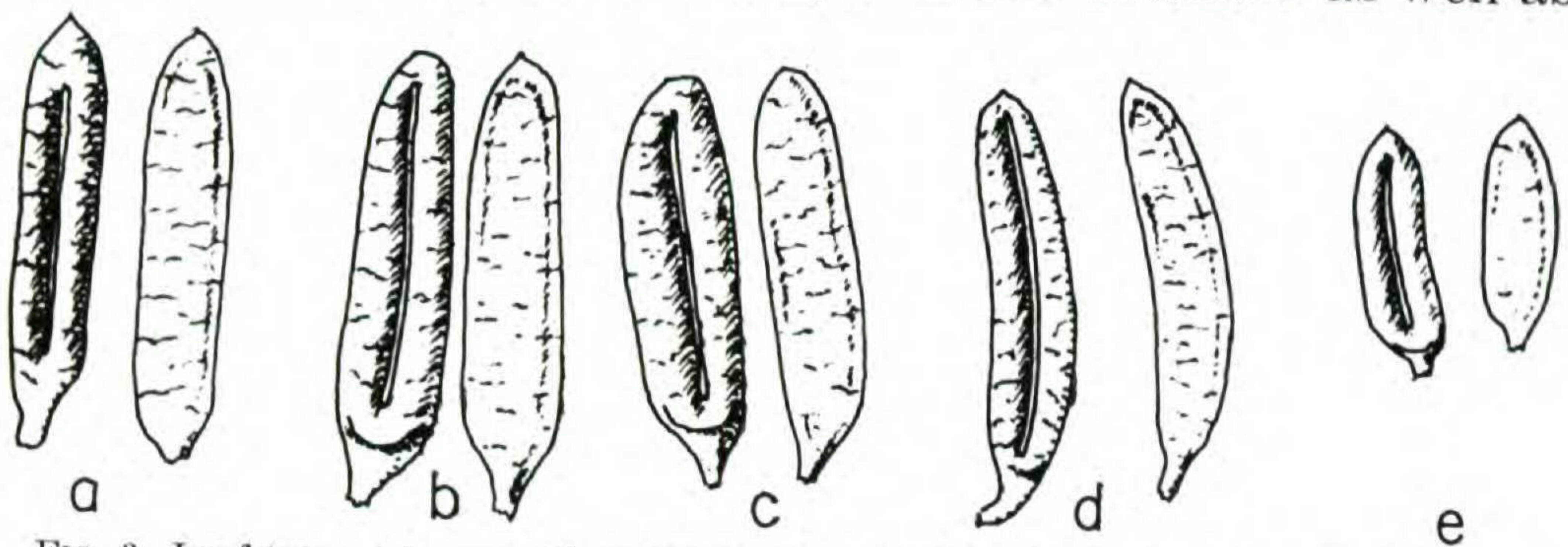


FIG. 3. Leaf-types of some *Empetrum*; left abaxial, right adaxial surfaces of: a) *nigrum*, b) *hermaphroditum*, c) "*purpureum*", d) *atropurpureum*, and e) *Eamesii*.

red-fruited taxa, the author could find no major, significant differences between the structure of the leaves (fig. 4), but some slight variation was noted in the width and firmness of the palisade layer and the thickness of the wax-coating (see above). The *nigrum* leaves (from Scania, Sweden) appeared to have the least well-developed palisade layer and collapsed easily under the pressure of the knife (fig. 4b). The *hermaphroditum* leaf (from Quebec province, Canada) was firmer (fig. 4c) but the relatively oval leaves of *E. rubrum* (from the Falkland Islands) and *E. Eamesii* (from Newfoundland, Canada) were the firmest of them all (fig. 4a, e). All leaves come from herbarium specimens, were soaked and then sectioned.

Good (1927) put a good deal of emphasis on the leaf shape of the various taxa, and so did Vassiliev (1949) in his study of the crowberries of the Northern Hemisphere. Generally it seems to us that the leaves of the Southern Hemisphere taxa are broader than those of the northern taxa, but in this respect *E. rubrum* f. *medium* (Tristan da Cunha, Gough

Island) with its long, narrow and apiculate leaves is an exception in the south, and *E. Eamesii* (Newfoundland and Labrador, Canada) with its short, slightly oval leaf is an exception in the north.

Remarks on the ecology of the red-fruited taxa: Ecologically, *E. Eamesii* seems to prefer dry, exposed slopes and summits of mountains, grows easily over rock and on rock-ledges as

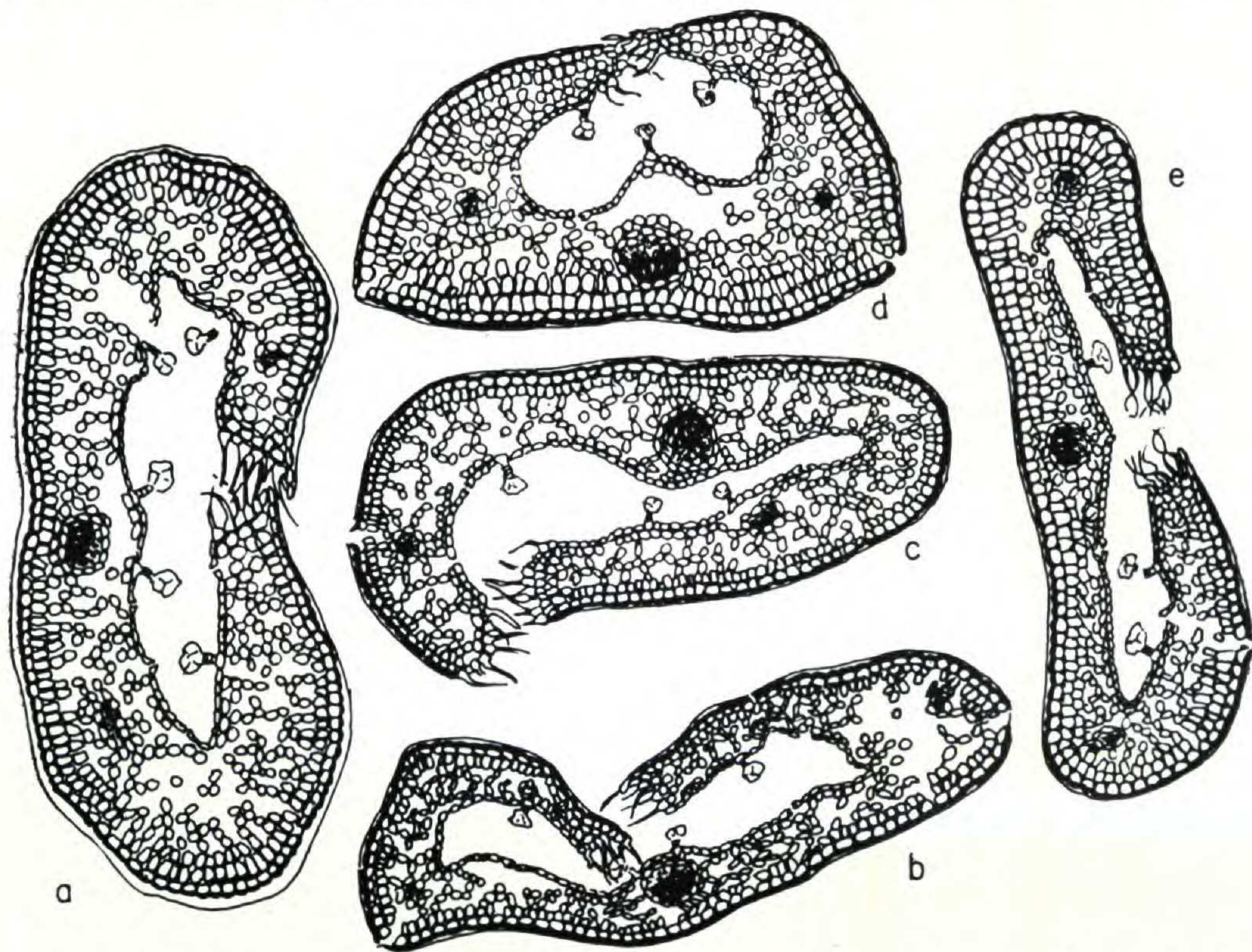


Fig. 4. Leaf-sections of some *Empetrum*: a) *rubrum*, b) *nigrum*, c) *hermaphroditum*, d) *atropurpureum*, and e) *Eamesii*.

well as on fine, angular gravel (La Pylaie, 1825; Eames, 1909; Fernald & Wiegand, 1913; E. Rouleau, pers. comm.) in contrast to the often boggy habitats of *E. hermaphroditum*. Only at Sheffield Lake, Eastern Brook, Green Bay district, Newfoundland (no. 2648, Aug. 1951, Rouleau) was *E. Eamesii* found on sandy beaches. It is closely bunched, with upright branches and forms a dense mat. The yearly shoots are very short, and the whole plant gives a strong impression of compactness. Few other plants mingle in its dense mats.

E. atropurpureum in mountainous areas seems to differ

in the same manner from *E. hermaphroditum*, i. e., in its absence from boggy and swampy areas and its preference for rocky ledges, exposed gravel and schist as well as decomposed granite with very little organic matter (Fernald & Wiegand, 1913). It is often found at or above timberline in high mountains.

On Mt. Washington, N. H., *E. atropurpureum* was collected in July 1959 on "frost-terraces" of loose gravel on the outer edge of the "Alpine Garden" (ca. 5000 ft. alt.) by Dr. M. S. Morrison, Uganda, on a joint excursion with this author and Drs. A. Löve, Montreal, L. C. Bliss, Urbana, Ill., and A. Medwecka-Kornas, Krakow, Poland. There may be a characteristic association of plants on these "frost-terraces" although no particular study was made to determine if this was so when the plants were collected. The *Empetrum* there, however, was noted to form small isolated mats and its branches were flattened against the terrace. This may have been due to wind sweeping up the hillside and may indicate a phenotypic growth-form, but cultivation of the plants would reveal to what degree it is a real genetic character. The trailing habit was also noted in some other herbarium specimens from Mt. Washington (C. G. Boott's Spur, July 1910, Forbes; along the carriage-road, coll. A. S. Pease, 1910; near the cog-railway, June 1941, Rousseau & Dansereau).

E. hermaphroditum on Mt. Washington is also mat-forming but has not been observed as trailing. It is very common on the mountain and is often a member of the relatively well-developed heath on the east- and south-facing slopes at about 5200 - 5700 ft. altitude, usually in the lee of rocks and krumholz. Other members of this community are: e. g. *Ledum groenlandicum*, *Vaccinium gaultherioides* (syn.: *V. microphyllum*, *V. uliginosum* v. *alpinum*), *V. Vitis-Idaea* ssp. *minus*, with smaller amounts of *V. caespitosum*, *V. angustifolium*, *Kalmia polifolia*, and at the lowest alpine levels, some *Betula glandulosa* v. *rotundifolia* (Bliss, pers. comm.; also observations by the author).

Along the shores of the River and Gulf of St. Lawrence, *E. atropurpureum* is often found growing on sand dunes, but also on granite rock (Fernald & Wiegand, 1913; Lewis, 1932), and the same, sandy or rocky, habitats are found in

its coastal area in Nova Scotia and Prince Edward Island. Everywhere it exhibits the loose, trailing growth, but a certain amount of wind pressure is active in all these habitats.

About the habit and ecology of *E. purpureum* we know next to nothing, but most likely it does not differ from that

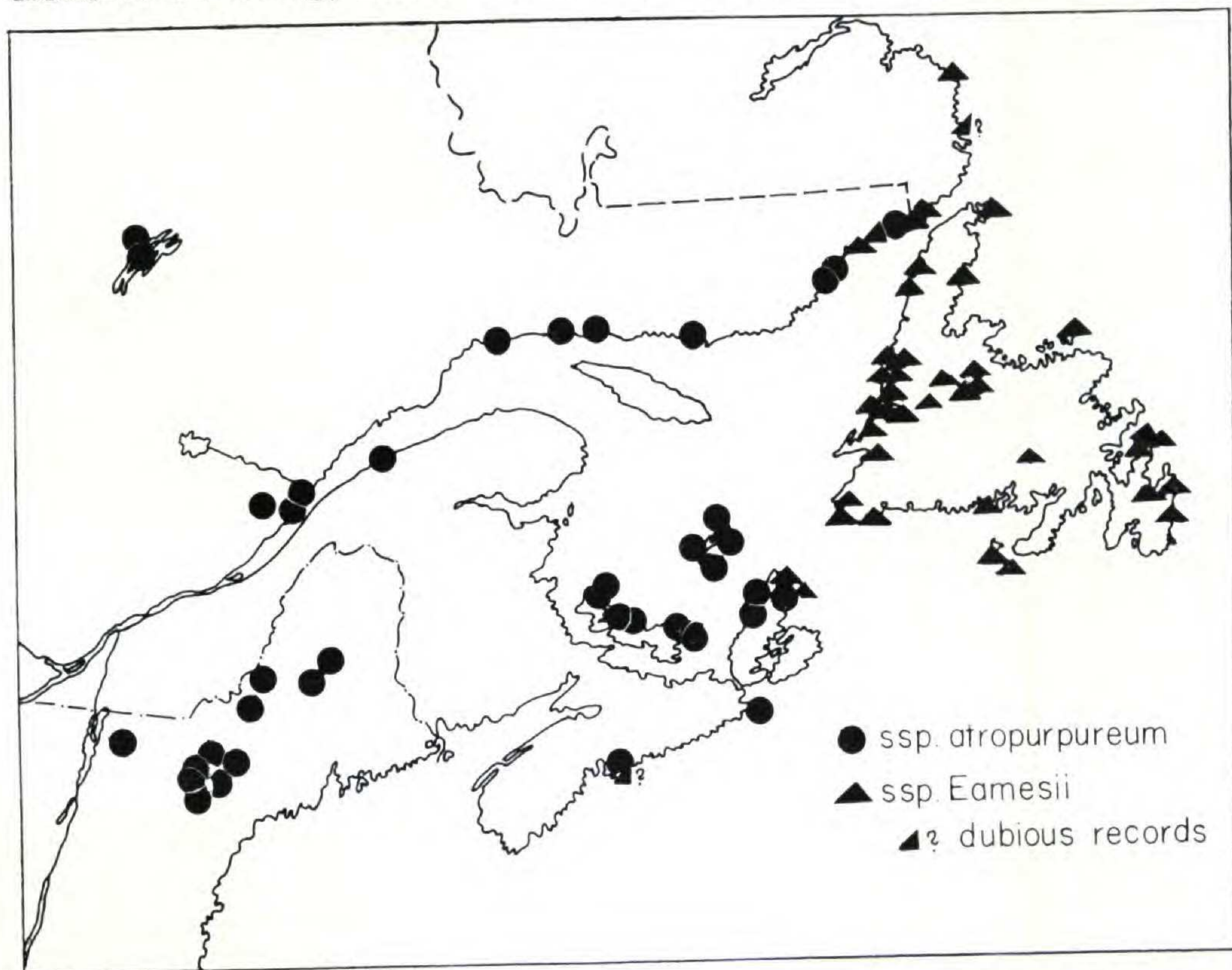


FIG. 5. Map of the distribution in eastern North America of *Empetrum Eamesii* ssp. *Eamesii* (triangles) and ssp. *atropurpureum* (dots). The latter is also found around the western end of Lake Superior in Minnesota and Ontario.

of ordinary *E. hermaphroditum*. Simmons (1906) stated about his collection of red-fruited *Empetrum* on Ellesmere-land: "I found this species within a limited area, where, however, it was rather abundant, and, as previously mentioned, covered wide stretches of peaty ground in the valleys, forming together with *Cassiope* and *Myrtillus*, a kind of heath." In its more southern localities it seems to have a preference for rock, similar to that of *E. atropurpureum*. At Bic, Quebec, on the south shore of St. Lawrence River, the habitat was indicated as "rocher" (=rock) for a specimen collected by J. Rousseau, and at Mt. Fortin, Matan Co., Quebec, Fernald and Pease noted as habitat "hornblende schist near the summit about 1100m. (3600 ft.) alt."

Distribution of the red-fruited taxa in North America: The three red-fruited taxa are sympatric with, although ecologically slightly different from, *E. hermaphroditum*, they seem to be fairly well separated geographically from each other (Maps, figs. 5 and 7).

In eastern North America *E. atropurpureum* is found in the Green Mountains of Vermont [Mt. Mansfield, July 7, 1877, C. G. Pringle, and same locality, June 21, 1908, Nellie

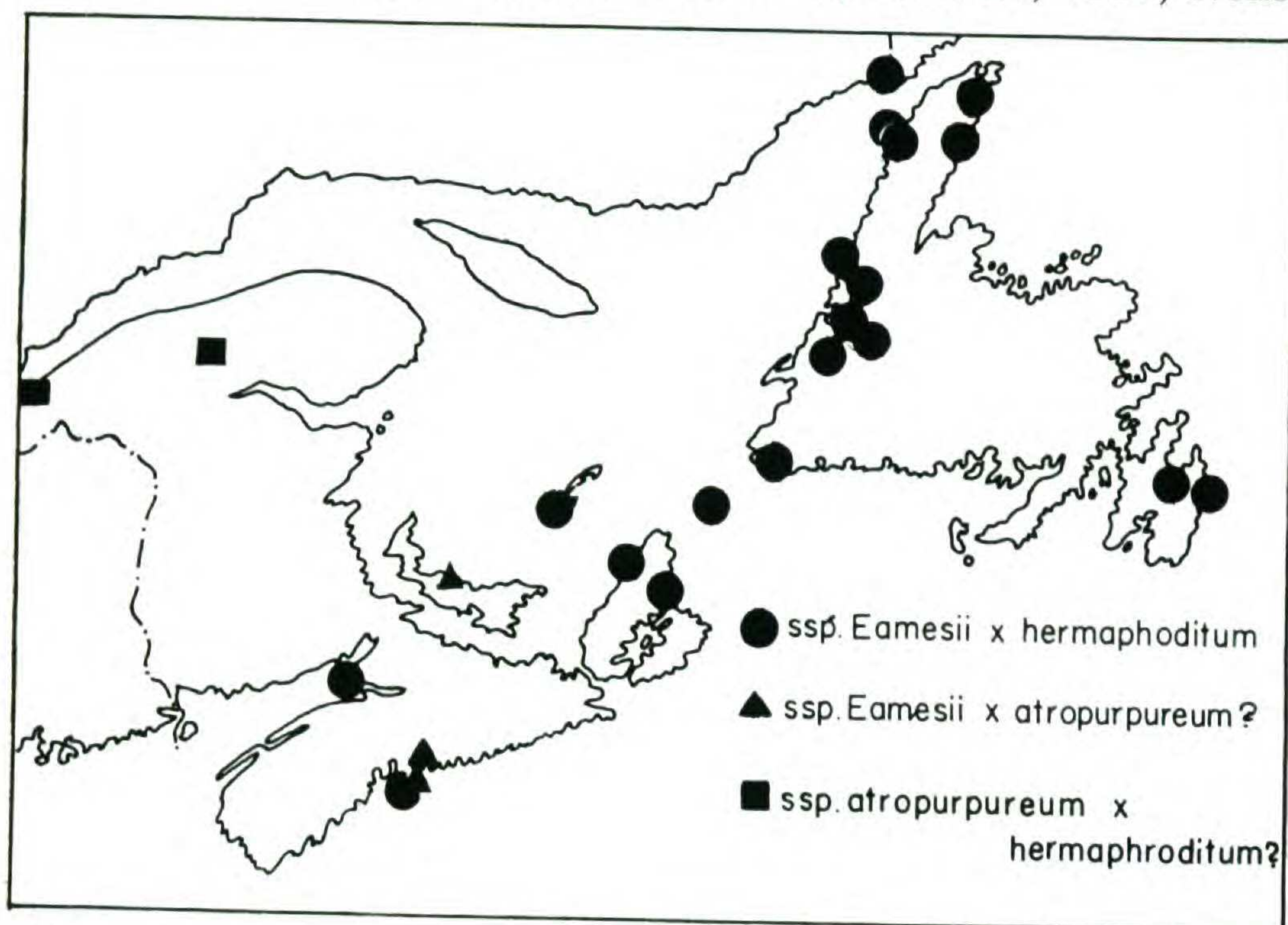


FIG. 6. Map of known localities of hybrids between *Empetrum Eamesii* ssp. *Eamesii* and ssp. *hermaphroditum* (dots), ssp. *Eamesii* and ssp. *atropurpureum* (triangles), and ssp. *atropurpureum* and ssp. *hermaphroditum* (squares).

F. Flynn (the latter was named *E. nigrum*, but is according to H. Vogelmann typical *E. atropurpureum*); in the White Mountains of New Hampshire, in the mountains of Maine and adjacent parts of Quebec province (but not on the mountains of the Gaspé peninsula), on both shores of the St. Lawrence River estuary as well as along the Gulf of St. Lawrence (north shore only, not on Anticosti Island), as far east as the border between Labrador and Quebec provinces at Blanc Sablon. Its northernmost localities, almost 250 miles north of the nearest known locality in Quebec province, are found at Lac Mistassini (no. 161, 1944, Rousseau &

Rouleau; no. 2083, July 1946, Rousseau). The absence of localities of *E. atropurpureum* between Lac Mistassini and the North Shore of St. Lawrence is possibly due more to the lack of collections from this area than to a real absence, but this can not be the cause for the absence of this taxon from the Gaspé peninsula and Anticosti Island, both of which have been well investigated by botanists.

This gap seems to continue down over New Brunswick, from which we have seen no collections, or any reports of *E. atropurpureum*. However, it reappears, and is quite common and often collected on Prince Edward Island as well as in the eastern parts of Nova Scotia and Cape Breton Island, and on Iles de la Madeleine (map, fig. 5; Fernald & Wiegand, 1913; Erskine, 1951). So far as we know it is absent from Newfoundland, the French Islands and St. Paul Island.

In central North America, there are a number of localities of *E. atropurpureum* around the western end of Lake Superior both in Ontario and Minnesota: Sailboat Island, Cook Co., Minn. (no. 339, Aug. 1937, Abbe & Abbe); Long Island, Twp 63N, R7E, Minn. (no. 517, Aug. 1937, Abbe & Abbe); Passage Island, Lake Superior (no. 107, W. S. Cooper in Fernald and Wiegand, 1913); Terrace Bay, N. Shore of Lake Superior, Ont. (no. 1168, July 1937, Hosie, Losee, Bannan); Heron Bay, N. Shore of Lake Superior, Ont. (no. 723, July 1939, Taylor, Bannan and Harrison). The latter two were collected as *E. nigrum* but later identified as *atropurpureum* by Baldwin. All these specimens look exactly like specimens from eastern U. S. A. and Canada.

The home of *E. Eamesii* is Newfoundland and the French Islands, St. Pierre and Miquelon, where the species is about as common as *E. hermaphroditum* (La Pylaie, 1825; Eames, 1909; Fernald and Wiegand, 1913). Outside this insular area, it occurs on the north coast of the Straits of Belle Isle (several localities in the county of Brouage between 57° and 58° W. Long.; cf. Fernald & Wiegand, 1913, Lewis, 1932), and as far north on the SE shore of Labrador as 53° 27' N. Lat. (Salmon Bight, no. 50, July 1937, Porsild).

One specimen from Greenland (Mudderbugtsdalen, Disko

Island, 69° 40' N., no. 392, Aug. 4 - 5, 1937, Porsild) looks superficially very much like an *E. Eamesii*, having hairy branches, small compact leaves densely set on the stems, but it lacks berries. Therefore, Dr. Porsild and this author have

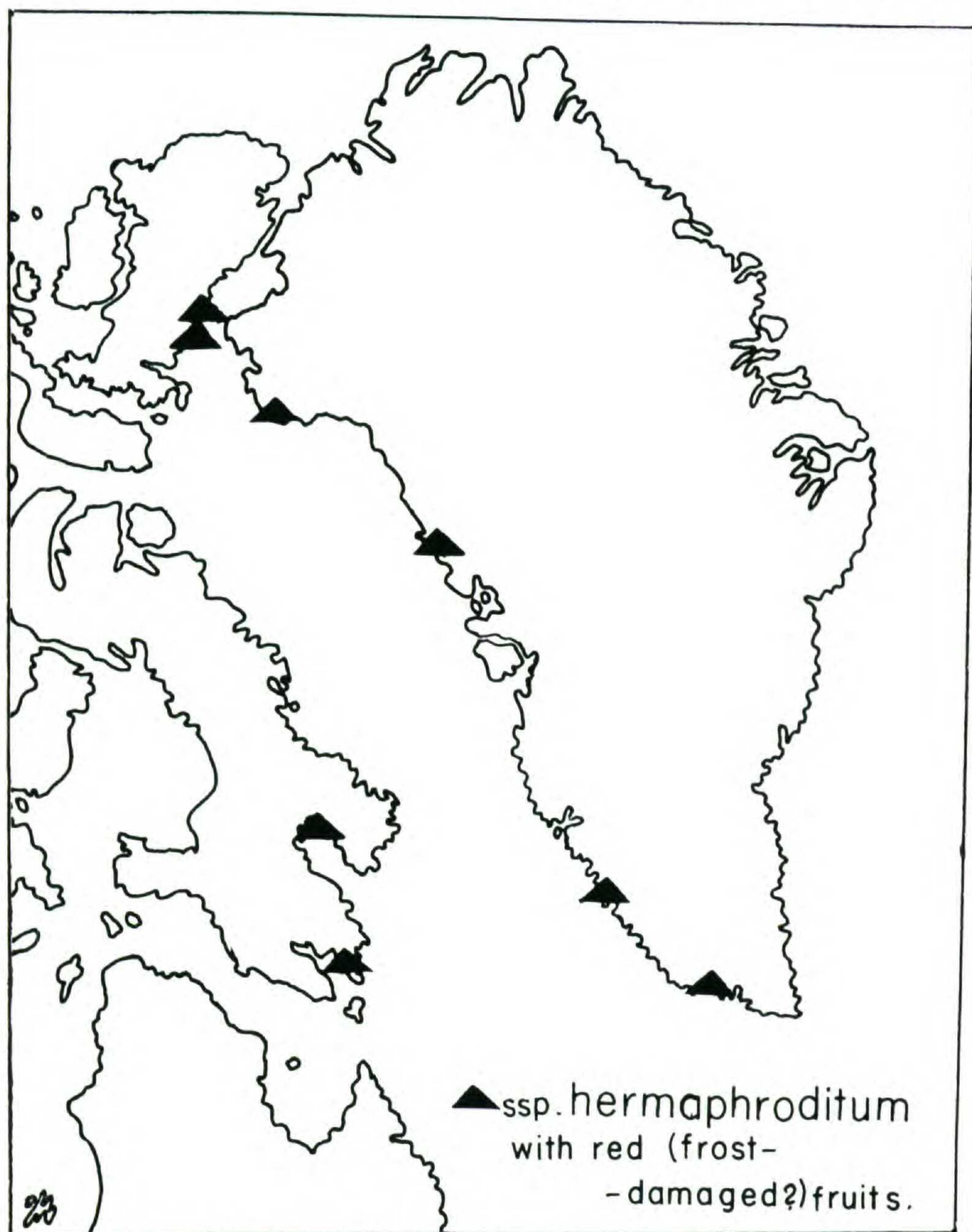


FIG. 7. Map of localities of arctic, red-fruited (frost-damaged?) *E. Eamesii* ssp. *hermaphroditum*.

agreed that until otherwise shown, *E. Eamesii* should not be considered as native to Greenland, and the particular specimen for the time being should be left as *Empetrum* sp.

E. Eamesii occurs also on the northern tip of Cape Breton Island (cf. Erskine 1951), and may possibly reach as far south as near Halifax, Nova Scotia. So far as we know, it has not yet been found on Iles de la Madeleine, or on St. Paul Island in the Gulf of St. Lawrence. For a map of the distribution of *E. atropurpureum* and *E. Eamesii* in eastern North America, see fig. 5.

It is slightly more complicated to define the area for what is purported to be the third red-fruited taxon, "*E. purpureum*", than for the other two. Fernald and Wiegand (1913) regarded it as arctic, but later Fernald changed his opinion both of its area and its taxonomical status. In 1923, he and A. S. Pease found specimens corresponding to Rafinesque's description growing on Mt. Fortin, Matane Co., Quebec. They had purple berries, and were, according to Fernald (1923), completely glabrous. However, we have been able to establish that the young twigs have a very sparse cover of curly brown hairs, and that the young leaves have a number of curly white hairs which seem to disappear soon. Compared to *E. atropurpureum* and *E. Eamesii*, this form can well be termed glabrescent.

Fernald (1923) named these specimens *E. nigrum* f. *purpureum* (Raf.) Fern. and suggested that it was nothing but an occasionally occurring form of *E. nigrum*, and not exclusively arctic.

The latter seems well supported by the discovery of additional specimens from Bic, Quebec (no. 24915, July 1926, J. Rousseau). This locality is on the south shore of the St. Lawrence River and the specimens are very similar to those collected by Fernald and Pease, having purplish fruits, a few white hairs on the youngest leaves, and some brown curly hairiness on the new twigs. Both the specimens from Bic and Mt. Fortin are hermaphroditic, and give an impression of being intermediate between *E. atropurpureum* and *E. hermaphroditum* (cf. map, fig. 6).

With the above mentioned collections in mind, it may be permissible to conclude that the "specimen from Labrador" on which Rafinesque (1838) based his description of *E. purpureum* originated from somewhere along the northern coast

of the Gulf of St. Lawrence, possibly from the present Quebec province, rather than from the truly arctic or sub-arctic parts of Labrador.

In the Herbarium of the Botanical Garden, Montreal, there is, however, a collection named *E. nigrum* f. *purpureum* from a truly arctic locality (Pangnirtung, Baffin Island, no. 1500, Sept. 1936, Dutilly), and another specimen with the same name is found in the herbarium of the Academy of Sciences, Philadelphia (York Sound, Frobisher Bay, 62° 35' N., 66°30' W., no. 862, July 1937, E. Perot Walker). These specimens do not seem to differ from those collected by Simmons on Ellesmereland (Simmons, 1906). His specimens are found in Oslo, Norway (no. 883, ad Cape Viele sinus Hayes Sound, Ellesmerelandiae orientalis, 4.VII.1899; no. 850, ad Twin Glacier Valley, sinus Hayes Sound, Ellesmereland orientalis, 6.VII.1899; both: leg. et det. Herman G. Simmons). Dr. J. Lid, Oslo, Norway, has given us the following information about them: Specimen no. 883 is flowering, but no. 850 has both flowers and berries. Both are hermaphroditic, glabrous and the fruits are shiny and red. Both sheets were revised in 1934 by Dr. Th. Arwidsson, Stockholm, Sweden, to "*E. hermaphroditum* (Lge.) Hagerup f. *purpureum* (Raf.) ?" The transfer has not been published.

Dr. A. E. Porsild, National Museum, Ottawa, has told this author in a letter that he has "from time to time picked up red-fruited specimens in various parts of the Arctic." Such red-fruited specimens do not only exist on the Canadian side of the Smith Sound - Baffin Bay - Davis Strait area, but also in Greenland. The National Museum, Ottawa, has the following collections: Danmark Havn, 76°45' N., July 16, 1908, Lundager; Godthaab, 64°11' N., June 25, 1930, Eugenius; Neria, 61°33' (three collections) a) July 16, 1930, b) July 2, 1924, c) July 4, 1926, Eugenius. All these collections have shiny red berries, are hermaphroditic, and have glabrous twigs. A fourth collection from Neria (June 26, 1927, Eugenius) is normal *E. hermaphroditum* as in the rest of Greenland.

In the Herbarium of the Academy of Sciences, Philadelphia, there is an old specimen from Greenland, which may

refer to some of those seen by Durand (1863) : Port Foulke, Dr. Kane's Expedition to the polar region, Sec. A. N. S. Vol. 3. — N. S. n^o 3, det. (as *E. nigrum*) I. I. Hayes. This specimen has no berries but differs in no way from ordinary *E. hermaphroditum*.

Both in a letter to the author and in personal conversation with her, Dr. A. E. Porsild, Ottawa has expressed his view that the red berries of these specimens may be the result of frost-bite or some disease, rather than a truly genetic character. A support for this theory may be found in a collection from Baffin Island (Cape Dorset, 64°10' N., 76°20' W., July 3, 1926, Soper), which appears to be partly frost-bitten, and which on the damaged side has exactly the kind of red, shiny, small berries as seen in the above-mentioned arctic specimens, but on the other half, fresh and green, has ordinary sized, bluish-black berries.

There seems thus to be some doubt about the true area as well as the true identity of what is named *E. purpureum*. A map, fig. 7, indicates the arctic localities mentioned above.

Hybrids between red- and black-fruited taxa: Strong evidence for an association of the red-fruited northern taxa with the *hermaphroditum*-complex rather than with the *rubrum*-complex is the fact that hybrids occur between them and *E. hermaphroditum*. The hybrids have either black, dark purple (most common) or purple fruits and are intermediate or approach one parent more or less in characters such as leaf size, hairiness and growth habit.

Fernald and Wiegand's (1913) description of *E. atropurpureum* is actually so broad, especially regarding fruit-color ("rubris vel atropurpureis opacis"), that most likely some hybrids between red-fruited and black-fruited plants fall into the group of dark-purplish-fruited ones. Thus it is rather hard to judge where the actual limit between the true *E. atropurpureum* and the hybrid between it and *E. hermaphroditum* should be drawn. There is probably a certain amount of introgression between the two, at least in Maine and New Hampshire.

On Newfoundland the situation is more clearcut, and several localities have yielded plants of distinct hybrid appear-

ance between *E. Eamesii* and *E. hermaphroditum* as well as many others showing signs of introgression between the two taxa (Table I). From the mainland north of Newfoundland on the border between Quebec and Labrador at Blanc Sablon two sets of hybrids have been collected (nos. 113 and 114, Aug. 1939, Brunel; cf. Table I), and it is interesting that at the time of collection, according to the label on sheet no. 113, a note was made: "Feuillage de *E. Eamesii*. Fruits: couleur de *E. nigrum*, goût de *E. Eamesii* (fide H. Lewis)". Another hybrid, at Venison Tickle, Labrador, (no. 13719, 1896, Waghorn) was collected under the name *E. nigrum*, but later re-determined first to *E. Eamesii*, then to *E. atropurpureum*.

Also south of Newfoundland a few hybrids between *E. Eamesii* and *E. hermaphroditum* have been discovered and are represented in the herbaria (cf. Table I) from localities on Cape Breton Island. They are all in the vicinity of both parent species.

On Iles de la Madeleine, in the Gulf of St. Lawrence (no. 9406, Ile Havre-Aubert, Marie-Victorin and Rolland-Germain) and on St. Paul Island (no. 53554, Aug. 1953, Erskine) specimens have been collected which have dark fruits, but leaves strikingly like those of *E. Eamesii*. However, so far as we know, no pure *E. Eamesii* has been collected or reported from any of these islands, but both *E. atropurpureum* and *E. hermaphroditum* are found there. It is not completely excluded that also *E. Eamesii* could exist there, but is rare and has escaped attention from botanists. A long range dispersal of pollen of *E. Eamesii* from either Newfoundland or Cape Breton Island to these islands does not seem reasonable, but hybrid berries and seeds could possibly have been carried by birds over these relatively short distances.

All the above-mentioned hybrids, usually named *E. nigrum* by their collectors, are hermaphroditic or, rarely, polygamous with a few female flowers on the same bush as the hermaphroditic.

A map of the known localities of the hybrids between *E. Eamesii* and *E. hermaphroditum* is given in fig. 6.

Hybrids between red-fruited taxa: Only two areas are known where *E. Eamesii* and *E. atropurpureum* overlap. One is on

the north shore of Belle Isle Strait on the border between Canada and Labrador (see map, fig. 6) but from this area we have so far seen no material that shows any sign of hybridity between the two red-fruited taxa.

The other point of contact seems to be on the northern tip of Cape Breton Island, from where specimens are known of both *E. atropurpureum* (several collections) and *E. Eamesii* (Lockhart Brook, Salmon River, Victoria Co., no. 6356, July 1952, Smith Taylor, Webster Slipp; Ingonish

TABLE I.

List of specimens showing hybrid traits between *Empetrum Eamesii* ssp. *Eamesii* and ssp. *hermaphroditum*. MT=Herbarium of the University of Montreal, OTT=National Museum, Ottawa, DAO=Department of Agriculture, Ottawa, PH=Academy of Natural Science, Philadelphia. **Labrador:** Venison Tickle, no. 13719, Waghorn, 1896 (OTT). **Quebec:** Blanc Sablon, nos. 113 & 114, Aug. 1939, Brunel (MT). Iles de la Madeleine, Ile Havre-Aubert, no. 9406, Marie-Victorin and Rolland-Germain (MT). **Newfoundland:** St. Anthony, Cremailliere Bay, no. 3029, Sept. 1951, Saville (DAO). St. John's Island, no. 4122, Aug. 1955, Rouleau (MT). Roddickton, Cloud Hills, no. 4619, July 1958, Rouleau (MT). Sally's Cove, Martin Point, no. 4766, July 1958, Rouleau (MT). Main Arm, Bonne Bay, July 1922, Fernald, Long, Fogg (MT). Killdevil Mt., Bonne Bay, no. 185, Aug. 1929, Fernald, Long, Fogg (PH). Mt. Musgrave, no. 392, Aug. 1948, Rouleau (MT). Stag Hill Brook, no. 1187, Aug. 1950, Rouleau (MT). Taleville, no. 4531, July 1958, Rouleau (MT). Trinity Bay, Old Perlican, no. 42, Aug. 1914, Torrey (OTT). St. John's, no. 150, Aug. 1894, Robinson & Schrenck (MT, OTT). Dog Peninsula, St. Margaret Bay, no. 28648, Aug. 1925, Fernald, Wiegand, Long, Gilbert Jr., Hotchkiss (PH). Port aux Basque, no. 26820, July 1924, Fernald, Long, Dunbar (PH). **Nova Scotia:** St. Paul Island, no. 53554, Aug. 1953, Erskine (DAO). Ciboux Island, Victoria Co., no. 10930, July 1954, Smith, Taylor, Schofield, Webster, Slipp, Bentley (DAO). Lockhart Brook, Salmon River, Vict. Co., no. 5358, July 1952, Smith, Taylor, Webster, Slipp (DAO). Spicer's Cove, Cumberland Co., no. 4846, June 1954, Bentley, Schofield (DAO). Sambro, Halifax Co., no. 26, Aug. 1940, Dore (DAO). Barrens, Victoria Co., no. 4612, July 1951, Smith, Schofield, Sampson, Bentley). From this area no hybrids have been noted so far, but from further south, some obvious ones have been seen.

Some specimens, named as *E. Eamesii* by the collectors, from Halibut Cove, Halifax Co., Nova Scotia (nos. 45526 and 45528, July 1945, Dore, Senn, Gorham) and from Sambro, Halifax Co., (no. 27, Aug. 1940, Dore) are rather aber-

rant from *E. Eamesii* as otherwise known. Their leaves are much longer and narrower than ordinary in *E. Eamesii* and remind one much more of *E. atropurpureum* leaves, but they are densely arranged on the stem, and all directed upwards as is common in *E. Eamesii*. The young twigs are lanate and the fruits are light pink, the latter fact also noted on the sheet by Dr. W. G. Dore of Ottawa. In growth habit they are all intermediate between the loose, trailing type of *E. atropurpureum*, and the more compact type of *E. Eamesii*.

The same characters are found in a specimen from Stanhope, Queen's Co., Prince Edward Island (no. 45322, June

TABLE II.

List of specimens showing hybrid traits between *Empetrum Eamesii* ssp. *Eamesii* and ssp. *atropurpureum*. **Nova Scotia:** Halibut Cove, Halifax Co., nos. 45526 & 45528, July 1945, Dore, Senn, Gorham (DAO). Sambro, Halifax Co., no. 27, Aug. 1940, Dore (DAO). **Prince Edward Island:** Stanhope, Queen's Co., no. 45322, June 1945, Dore, Gorham (DAO).

1945, Dore & Gorham). Also in this case Dr. Dore has noted the remarkably intermediate traits on the determination label.

All of the above-mentioned specimens can hardly be anything but hybrids between *E. atropurpureum* and *E. Eamesii*. The map in fig. 6 shows the localities. The specimens are listed in Table II.

DISCUSSION AND TAXONOMICAL REVISION

Reviewing what has been said above we find that the basis for a relationship between the North American red-fruited taxa and the South American *E. rubrum*-complex consisted of similarities in fruit-color, hairiness, and, in one case, leaf-shape (Good, 1927).

Our own reasons for establishing a bond with the *E. hermaphroditum*-complex instead are based upon the facts that the red-fruited, North American taxa are sympatric with *E. hermaphroditum*, are hermaphroditic (or polygamous) like it, and seem to hybridize with it. These facts appear to us a better foundation on which to build an understanding of relationship than mere similarities in morphological characters.

We do not know yet whether it is possible to cross the red-fruited North American taxa with the South American ones,

but since at least the majority of the latter are dioecious, there ought to be as effective a barrier as that between the dioecious, diploid *E. nigrum* and the hermaphroditic, tetraploid *E. hermaphroditum*. In addition, the disjunction of the Southern and Northern Hemisphere taxa must have occurred in a geologically remote period, and Fernald's somewhat over-enthusiastic idea of a preglacial, cold-period, mountain-top-migration of the red-fruited taxa from New England down to Chile (Fernald, 1902) must be discarded as completely unrealistic. Most likely Fernald himself dropped this idea; at least he never again mentioned anything regarding the migratory tendencies of *Empetrum*.

Actually *Empetrum* disperses very slowly. The seeds are difficult to germinate and require several months to several years in the ground before they will develop. Their germination rate, whether before or after passage through an animal, is very low (Hegi, 1908; Hagerup, 1922). The vegetative shoots grow only 10 to 15 cm. per year as measured in Denmark (Hagerup, 1922), 3 to 4 cm. per year in Greenland (Menz, 1912), and probably not much more elsewhere. Individual plants can, however, cover a considerable area, and stems up to 80 (Hegi, 1908) and 140 (Good, 1927) years old have been reported.

It is much more likely that the red-fruited taxa in the Northern Hemisphere are the result of an independent, but much later occurring evolution only grossly comparable to that in the Southern Hemisphere. In both cases, independent genes for fruit-color, hairiness and habit could have mutated, but it is also possible that a whole group of genes, involving all these characters could have been affected at once (cf. Good, 1927). However, since at least in the Northern Hemisphere, we have various degrees of change (fruit-color, hairiness: *E. atropurpureum*; fruit-color, hairiness and leaf-shape: *E. Eamesii*), it seems that here several mutations involving different genes might have taken place independently in time and space.

It is tempting to relate the existence of the red-fruited taxa, as they occur in northeastern North America, to the events of the Pleistocene Ice Age. Such a correlation might be made in view of the relatively restricted areas where al-

most no overlapping occurs as in the case of *E. Eamesii* and *E. atropurpureum*. The former may have appeared rather late (before or during the Wisconsin glaciation?) in Newfoundland, and barely have had time to gain a foothold on the mainland, whereas the latter might have had its origin south of the ice rim (or have been pushed south with the boreal flora in front of it? cf. the disjunct area New England—Minnesota.), and later been able to follow it somewhat northward as the ice withdrew.

In the case of the three taxa, *E. hermaphroditum*, *E. Eamesii* and *E. atropurpureum*, there is no doubt that they are closely related, especially since they seem to hybridize freely. They cannot, in spite of certain differences in fruit-color, habit and area, be regarded as distinct species, but must be fused into one single species as three separate subspecies (Du Rietz, 1930). Biologically, the wide-spread, black-fruited, hermaphroditic taxon must be regarded as the taxon from which the two red-fruited taxa have developed. It would be nice if the oldest name applied to this primitive group. However, of the three taxa in question *E. Eamesii*, as well as *E. atropurpureum*, were both recognized and described at the specific level (Fernald & Wiegand, 1913) at an earlier date than *E. hermaphroditum* (Hagerup, 1927). Therefore one of the two first-mentioned names must designate the species (according to article 57, International Code of Nomenclature, 1956). We are free to choose between the names of the two red-fruited taxa, as both were published on the same date and on the same page (cf. article 58A, recommendation 3). Therefore, we are selecting *E. Eamesii* Fern. & Wieg. as the species name both because it designates a well delimited taxon and because the name is noncommittal as to morphological characters.

The following nomenclatural revision is made in conformity with the International Code of Nomenclature:

EMPETRUM EAMESII Fernald & Wiegand

1. ***E. Eamesii*** Fernald & Wiegand ssp. ***Eamesii***
E. rubrum sensu La Pylaie in *Terrae-Novae*; *E. rubrum* Vahl ssp. *Eamesii* (Fern. & Wieg.) R. Good.

2. ***E. Eamesii*** Fernald & Wiegand ssp. ***atropurpureum*** (Fernald &

Wiegand) D. Löve stat. nov. based upon *E. atropurpureum* Fern. & Wieg. in *Rhodora* 15: 215. 1913. *E. rubrum* Vahl var. *atropurpureum* (Fern. & Wieg.) R. Good.

3. *E. Eamesii* Fernald & Wiegand ssp. *hermaphroditum* (Hagerup) D. Löve stat. nov., based upon *E. hermaphroditum* Hagerup in *Dansk Botanisk Arkiv* 5 (2): 14. 1927. *E. nigrum* L. β *hermaphroditum* Lange nom. nud.; *E. nigrum* var. *hermaphroditum* Sörenson.

The situation is difficult as regards the so-called "*E. purpureum*", especially because the application of this name remains obscure. It seems possible that the plants which Rafinesque (1838) had in mind were of the type collected later by Fernald and Pease on Mt. Fortin, Quebec (Fernald, 1923), and by Rousseau at Bic on the St. Lawrence River estuary south shore, and which can possibly also be found in other places, including southern Labrador, along the Gulf of St. Lawrence. In this case it is most probable that these plants were the result of hybridisation between e. g. ssp. *atropurpureum* and ssp. *hermaphroditum* (map, fig. 6). This explanation can not, however, be used to explain the existence of purported "*E. purpureum*" in Baffinland, Ellesmereland or Greenland (Durand, 1863; Simmons, 1906; Porsild, pers. comm.; own observations). Neither is there a reason to believe that the plants which we here have referred to as "*E. purpureum*" have a disjunct area split in two by e. g. the Wisconsin glaciation. A hypothesis that the red fruits of the arctic plants are the result of damage by frost, as proposed by Dr. A. E. Porsild, Ottawa, in a discussion with this author, seems to us the most likely one in case of the northern plants (map, fig. 7).

Rafinesque (1838), in describing the fruits of his "*E. purpureum*" used the word "red" as well as "purple", but also indicated that the "red" color was that of *Phytolacca*, the fruits of which certainly have a purplish hue (cf. Fernald & Wiegand, 1913; Fernald, 1923). It is therefore likely that his plant did not belong to the arctic type with shiny red fruits, looking as if they were polished. The arctic plants may still belong to a race occurring around the Smith Sound — Davies Strait area, which responds to frost with a color change of its fruits, but till established that this is so, they are better regarded as monstrosities of ssp. *hermaphroditum*.

Both because of its generally vague application and because the name has more than once been applied to heterogeneous material (in one case to a suspected hybrid, in another to a monstrosity) the name *E. purpureum* Raf. must be rejected on basis of articles 63, 65 and 67, International Code of Nomenclature, 1956.

The following key may be used to identify the taxa discussed above:

- A. Plants hermaphroditic, or polygamous with bisexual and female, rarely male, flowers on the same plant.....B.
- B. Fruits red or purplish; young twigs densely white-hairy....C.
- C. Fruits bright red, opaque; leaves short, ca. 2.5 - 4 mm. long, oval, crowded, erect or ascending..... *E. Eamesii* ssp. *Eamesii*.
- C. Fruits dark red or purplish, not opaque; leaves long, ca. 4 - 6 mm., linear, ascending or soon divergent, not crowded.....
..... *E. Eamesii* ssp. *atropurpureum*.
- B. Fruits black, often with a bloom; leaves long-linear, soon reflexed; young twigs glabrous or with a short brownish fuzz.....
..... *E. Eamesii* ssp. *hermaphroditum*.
- A. Plants with male or female flowers on separate plants; fruits black, often with a bloom; twigs glabrous; leaves long-linear, soon reflexed..... *E. nigrum*.

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